Sex Ratios in Pigeons, together with Observations on
the Laying, Incubation and Hatching of the Eggs.

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CONTENTS.

AGRICULTURAL EXPERIMENT STATION OF THE RHODE ISLAND STATE COLLEGE.

SEX RATIOS IN PIGEONS, TOGETHER WITH OBSERVATIONS ON THE LAYING, INCUBATION AND HATCHING OF THE EGGS.*

BY LEON J. COLE AND WILLIAM F. KIRKPATRICK.

Introduction.

The results presented in the present paper have been obtained in the course of studies on inheritance in pigeons, two reports on which have already appeared (Cole, 1914; Lloyd-Jones, 1915). As in the first of these, the data in the present instance have resulted from experiments begun at the Rhode Island Agricultural Experiment Station in 1907, and continued by the senior author at the Wisconsin Experiment Station since the summer of 1910. It is only fair to state that the junior author† had practically full charge of keeping the field notes and taking records up to July, 1910, though the senior author made practically all the descriptions and determinations of sex. All sex determinations are based on the performance of birds which have actually bred, or on dissections. In no case has sex been recorded from the behavior of young birds, unless so verified later.

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†Now Professor of Poultry Husbandry, Connecticut Agricultural College, Storrs, Conn.

Since July, 1910, the birds have been more constantly under the observation and care of the senior author, but acknowledgment should be made to Mr. J. C. Curtis and Mr. F. J. Kelley who have at different times assumed a large part of the responsibility for the daily records. Upon the senior author also has devolved the entire writing of the present report.

The subjects here brought together are somewhat disconnected, but for various reasons it seems best to present such data as are available upon them at the present time. The sex ratio in pigeons, and the relation of sex to the order of laying of the eggs are of especial interest because of the prevailing popular notions on the matter, and the fact that these ideas, if true, would be very difficult to explain on the basis of our present knowledge of sex determination and the physiology of egg production in general. As for the time of laying and the time of hatching of the eggs, no statistics we believe have ever been published on these points, though general statements are common in the literature. Our knowledge of the maturation process and the earliest stages of avian embryology are, moreover, based very largely on studies made on the egg of the pigeon, and all accurate information which can be obtained on processes of egg production may be of service in this connection. A knowledge of the most probable time of laying of the second egg may especially be of use in obtaining desired maturation stages. Finally, although the results of the present investigation are largely destructive of the popular notions of sex determination and sex control in pigeons, it is always an advantage for the practical breeder to know the facts, since a knowledge of them may save him much time and effort along fruitless lines.

Investigation on certain of the subjects discussed in this paper is being continued by the Department of Experimental Breeding at the University of Wisconsin, and will subsequently be reported more fully.

Sex Ratio in Pigeons.

Hyperandry, or an excess of males, among pigeons has often been noted, and is occasionally mentioned in current articles on pigeons. It appears to be a matter of common belief among pigeon raisers, in fact, that the males exceed the females in number, and we find the same fact mentioned by Darwin (1875, p. 247), who says: "In regard to domestic pigeons there is good evidence either that the males are produced in excess, or that they live longer; for these birds invariably pair, and single males, as Mr. Tegetmeier informs me, can always be purchased cheaper than females." Darwin submits no definite figures, however, in support of his conclusion. We have, moreover, been unable to find any published figures on the sex ratio of pigeons, except those by Cuénot (1900), who reported on 136 pigeons whose sex was determined soon after hatching. He found 73 males to 63 females, or a ratio of 115.87 to 100, which would mean a relatively pronounced over-production of males.

The proportion of males per 100 females found by Cuénot is considerably higher than we have obtained. Our results for birds of all ages, tabulated to December 24, 1910, were 292 males to 278 females, a ratio of 105.03 to 100. A later tabulation of all sexes determined to July 18, 1914, including the above, gives 845 males to 803 females. This ratio (105.23 to 100) is practically the same as that obtained at the earlier date and since the correspondence is so close, and the numbers are fairly large, it may be assumed that 105:100 represents closely the regular proportion of the sexes in the pigeons we have used.* While these are mostly what are known in this country as Long-faced Tumblers† (both Clean Legged and Muffed), our stock has been derived from various sources and includes also some Parlor Tumbler stock. In addition there are

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*A still later tabulation was made to December 1, 1914, which added 74 males and 78 females to the list, bringing the total number of known sexes up to exactly 1,800; of these, 919 were males and 881 females, or 104.31 : 100. This slight lowering of the ratio is probably not enough to affect significantly the statement made above.

†They correspond in type to the "Mittelschnäblige" rather than to the "Langschnäblige Tümmler" of the Germans (cf., for example, the illustrations in Schnaehtzabel, 1906).

included some, though comparatively few, records of other breeds, especially Homers, which have been used only to a limited extent in our studies. Considering the diversity of origin of the Tumbler stock and the other inclusions it seems quite probable that the ratio of 105 males to 100 females may be taken as the sex ratio for domestic pigeons generally.

Although the sexes have been determined at different ages in different birds, the combined figures give the sex ratio of all birds hatched whose sex has been determined. There are included, it is true, 81 birds that had not succeeded in emerging completely from the shell at time of death, but whose sex was nevertheless determined. They were therefore recorded technically as "dead in shell," rather than "hatched;" but for reasons which will appear it has seemed inadvisable to separate these birds from those which died within the first few days after hatching. Of these birds "dead in shell," 44 were males and 37 females; their exclusion would give a slightly lower ratio of males actually hatched, but the change would probably not be significant.

Is there a Differential Mortality ?

Darwin suggested two explanations for the apparent preponderance of males among adult pigeons; first, that males are produced in greater numbers; second that they live longer, or in other words, that there is a higher relative mortality among the females in early life.[*] The data here presented seem to show fairly conclusively that his first supposition is correct, that there is a slightly greater production of males; but it is doubtful if this excess is great enough to be noticed ordinarily and to account for the prevailing impression. As to a possible differential mortality, Darwin (1875, p. 247) states, on the authority of Mr. Harrison Weir, that when the nestlings are of opposite sexes, "the hen is generally the weaker of the two, and more

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[*]Aristotle (1910, 613[a] 24—29) says of ring-doves and turtle-doves, "The male, as a general rule, is more long-lived than the female; but in the case of pigeons some assert that the male dies before the female, taking their inference from the statements of persons who keep decoy-birds in captivity."

liable to perish." Cuénot (1899, p. 491) is the only author we have found who gives any actual data on this point. He states that while there may be some truth in the assertion it certainly is not general, for he examined two young pigeons which were less vigorous than their mates, and which the breeder assured him for that reason were females; in reality one was a female, but the other was a male. In another case he dissected two squabs from the same nest, one of which was very vigorous and should have been a male, the other was less developed, and therefore should have been a female; but this time both were females.

On this point we have 60 cases to report. These records were made at Wisconsin by Mr. F. J. Kelley, who has kindly tabulated them for us. They show the relation of sex to the relative size of the two squabs at the time of banding, which means at the age of 10 to 15 days. The cases recorded include only those in which there was a fairly well-marked difference in size, and in which the squabs had remained in the same nest and under the same conditions so far as could be told. The data may be summarized as follows:

Larger squab   ♂, smaller squab ♀..........23 cases.
    "   "   ♀,   "   "   ♂......... 4 cases.
    "   "   ♂,   "   "   ♂.........13 cases.
    "   "   ♀,   "   "   ♀..........16 cases.
    "   " Unknown,   "   "   ♂......... 2 cases.
    "   "   "   "   "   ♀......... 1 case.
    "   "   ♀,   "   "   Unknown....1 case.

Total sexes—large squab = 36 ♂♂ : 21 ♀♀
              small squab = 19 ♂♂ : 40 ♀♀
                            ─────────────────
                            55 ♂♂ : 61 ♀♀

These data certainly seem to lend considerable support to the idea that the larger squabs are in a significant majority of the cases males. A consideration of cases in which one squab died before banding shows less striking results. The argument in this case would be that the female squabs are smaller and less vigorous, more

of them would die than of males, and therefore there would be a correspondingly higher percentage of males at the time of banding. In the following pages these points are examined critically on the basis of a larger number of data, other age limits being used, however, than age at banding. Data to support this contention are furnished, and we have therefore examined our records with a view to determining its validity.

From our records to December 1, 1914, the age at time of death of 1,227 birds not including those killed can be determined, and for convenience these have been divided into four groups, one of which seems to have a natural basis, whereas the limits of the other three are more or less artificial. These may be defined as follows:

GROUP A. *Hatching period.* Embryos which were fully developed but which failed to hatch ("dead in shell") and birds which died within five days after hatching.

GROUP B. *Nestling period.* Squabs dying at from 6 to 28 days, inclusive.

GROUP C. *Immature or juvenile period.* Squabs living over 28 days, but dying before six months of age.

GROUP D. *Adult period.* All birds living to the age of six months or more.

Number
of deaths.
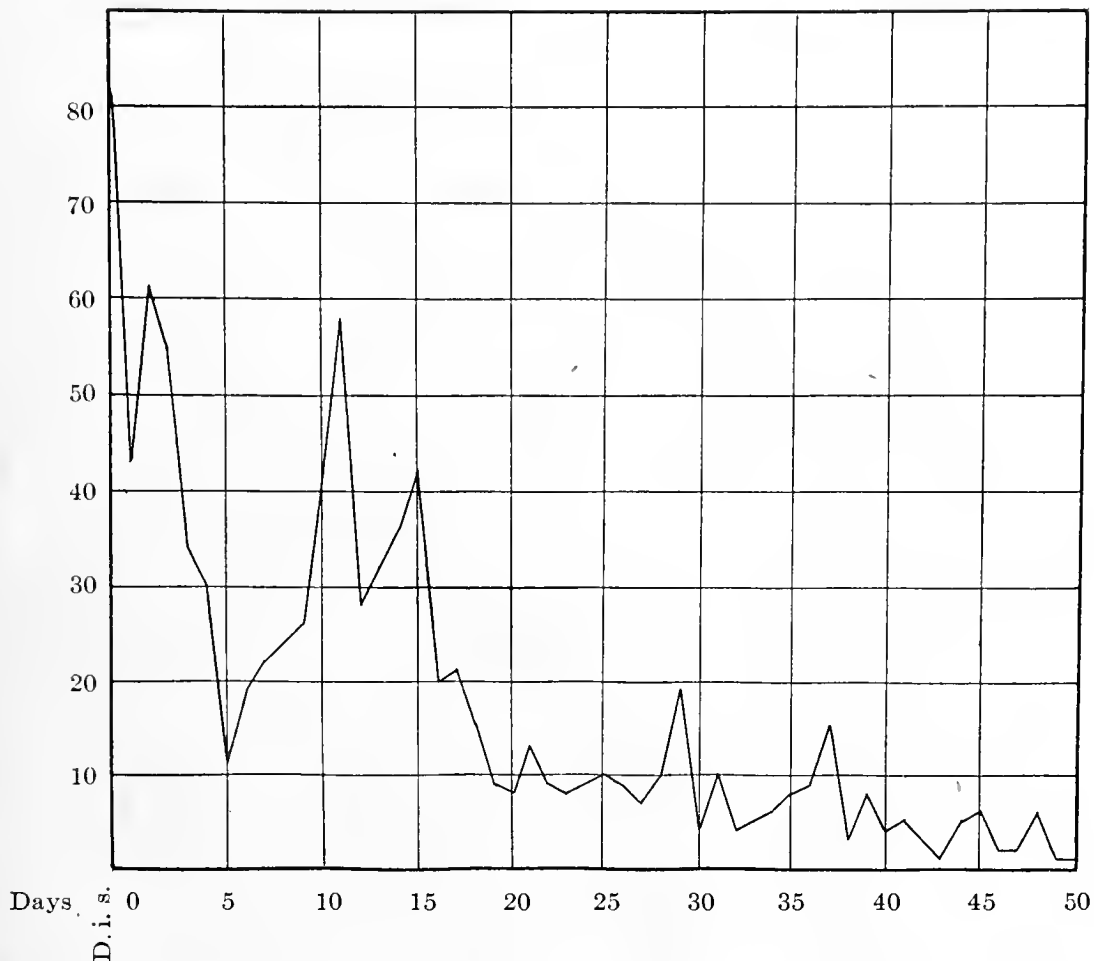
FIG. 1.   Number of squabs dying at each day of age up to fifty days.   D. i. s., dead in shell;
0, day of hatching; 1, one day old; etc.

In Figure 1 is represented the number of birds dying at each
age, at one day intervals, up to 50 days.   In the "dead in shell"
column only those embryos are included whose sex was determined.
The number of fertile eggs which failed for one reason or another
to hatch was, of course, very much larger.

Since records are systematically taken once daily, the recorded
age at death is usually correct within that period; in a comparatively
small number of cases a bird may have been dead for a somewhat
longer period before discovered, and there are included records of
some birds which were killed because so sick it was evident they would
not recover and that death would probably have intervened within
a short time.   These slight inaccuracies tend to offset one another,

and are of little or no consequence so far as the general results are concerned.

It has been found inexpedient to attempt any classification on the basis of the cause of death, since in so many cases this could not be determined and has not been uniformly recorded. Death may result from a great variety of causes, among which perhaps the most important are lack of constitutional vigor, neglect by the parents (especially during cold weather), specific infections, and accidents, especially those resulting from the fighting and interference of adult birds.

Figure 1 shows a high incidence of deaths at time of hatching which rapidly declines to a minimum on the fifth day, after which there is a correspondingly rapid rise to a marked mode from the tenth to fifteenth days. The first two or three days and the tenth to fifteenth days after hatching appear, therefore, to be the most critical periods in the life of the young squabs. The minor irregularities probably have little meaning, and in most cases no explanation is apparent, as for example, the much greater number of deaths on the eleventh day than on the twelfth. On the other hand the greater height of column 1 over the 0 column is probably due to the fact that many squabs living only a few hours after hatching are really not recorded as dead until the following day. There can be no doubt, however, that the marked depression in the death rate at the fifth and sixth days is of significance, and this point has therefore been chosen as the limit between the deaths at hatching and immediately following, and those grouped around the age of about two weeks. From this time the number of deaths drops off again rapidly, and the curve then swings out gradually to about 50 days, after which there is a steady but slight decrease in the number of deaths per month for the full period of nearly six and one-half years since the first squabs were produced in our experimental work. It must be borne in mind, however, that this gradual decrease in the number of deaths recorded does not necessarily imply a decreasing death rate, in fact probably the reverse is true. The death rate at any age should be based on the

number of deaths in proportion to the total number of individuals of that age, and this number rapidly decreases in our flock with advanced age as the birds die off, are killed, or are otherwise disposed of. Since therefore it would be very difficult or practically impossible for us to calculate the total population and age composition of our flock for the period under discussion, it is impossible to give any curve which represents accurately the death rate in our pigeons.

The point of interest which appears from the statistics (see Fig. 1) presented is that no such definite demarkations exist for separating Groups B, C and D from one another as marks Group A off from Group B. These groups were in fact established before the tabulation of deaths was made, on the basis of the life cycle of the birds. Twenty-eight days was taken as marking approximately the termination of the nestling stage, since at that age most squabs have left the nest. Six months was chosen arbitrarily for the beginning of the adult stage as representing approximately the average age at which pigeons are sexually mature and may begin breeding if conditions are favorable. It is true that a few early hatched birds may breed the same season, but the great majority do not begin until the following year.

With the above classification as a basis we may now examine the question of a differential mortality. In order to test the statement quoted from Darwin (p. 465) tabulations have been made of cases in which the two nestlings were known to be of opposite sex and one or both died before reaching adult life (period D). A total of 172 such cases is recorded: in 88 of these the male died first and was survived for a longer or shorter period by his female nestmate; in 84 cases the female died first and was survived by the male. Since these figures relate only to bisexual broods, the number of males and females hatched was equal, namely, 172 of each.* The excess of four male deaths over the female deaths is so slight as probably not to be significant, so we may say that the death rate for the two sexes was also essentially equal.

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*The excess of males hatched (in the ratio of 105 : 100; cf. p. 465) must be accounted for by an excess of male unisexual broods, or by a greater number of males among broods containing but a single squab.

In more than half the cases enumerated above, the surviving member of each pair of squabs failed to reach maturity; since both therefore died before six months of age, they in no way influenced the sex proportions in Group D.　Summarizing those cases in which one member of the bisexual pair of nestlings died before six months and the other exceeded that period we find a total of 68 examples,—31 in which the male died and the female survived, 37 in which the female died and the male attained the adult stage.　While the number of female deaths in Groups A, B and C is here somewhat larger, it should be borne in mind that the number of cases is relatively small, and that we are dealing only with bisexual broods which happened to meet these conditions.　So far as the above figures go, therefore, they seem to show that there is no marked tendency for one sex to be weaker than the other in bisexual broods, and there is only slight indication that male survivors may exceed female survivors in reaching the adult stage as here defined.

Table I.—*Composition of population and number of deaths with respect to sex in the different age periods.*

Age period.	Population.			Deaths.		Per cent. of population which died.		Ratio of ♂ deaths to 100 ♀ deaths.
	♂♂	♀♀	♂♂ : 100 ♀♀	♂♂	♀♀	♂♂	♀♀	
A........	866	810	106.9	115	114	13.3	14.1	100.9
B........	751	696	107.9	228	193	30.4	27.7	118.1
C........	523	503	105.0	135	142	25.8	28.2	95.1
D........	388	361	107.5	388*	361*	100.0	100.0	107.5

The distribution of deaths with respect to age and sex (using the age-groups which have been defined) is shown in Table I, the

*This does not mean that all these birds were yet dead at the time of tabulation, but when their death occurs it will of course be in this period.

age period at time of death being known for 1,676 birds* whose sex was determined as well. Of these 1,676 pigeons, 866 were males and 810 were females, the ratio being 106.9 : 100. While this ratio is slightly higher than that (105 : 100) which has been taken as normal, the difference is not great enough to be of much significance, and for present purposes we only therefore consider the changes in a population assumed to consist at hatching of 866 males and 810 females, all other birds being left out of consideration for the time being. In Period A, that is, within five days of hatching, 115, or 13.3% of the original number of males died, and 114, or 14.1% of the females. The number of deaths of each sex is almost equal (100.9 : 100), there being one more male death than female, but the *percentage* of female deaths is slightly greater.

Subtracting the deaths in Period A leaves the population in Period B composed of 751 males and 696 females, or 107.9 : 100, a slightly higher proportion of males than before. In this period the number of male deaths considerably exceeds the female deaths, there being 228 of the former and 193 of the latter (118.1 : 100). The proportion of the males which died in Period B is 30.4%; of the females, 27.7%. The distinctly higher death rate of males in the nestling period is reflected in the composition of the juvenile population (523 males, 503 females), where the proportion of males (105 : 100) is lower than at the start. Period C is the only one in which the actual number of female deaths exceeds the male deaths, and the only one in which the percentage of female deaths is in excess to any appreciable degree. The ratio of male to female deaths is 95.1 : 100; expressed in percents, 25.8% of the males composing the population died, 28.2% of the females. Allowing now for all previous deaths we find that the adult population (Period D), consisting of 749 birds, comprises 388 males and 361 females, or only a slightly, and probably insignificantly higher ratio of males (107.5 : 100) than that with which we started.

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*In addition to the 1,227 birds mentioned on page 468 there are here included those birds which were killed after they were six months of age, and birds over six months of age alive on December 1, 1914, whose sex had been determined by their breeding behavior. It is certain, therefore, that all these belonged to Group C.

A review of the proportion of males to females in the different age periods displays surprisingly little fluctuation, it never being greater than 107.9 nor less than 105. Certainly these differences are not great enough to account for the prevailing impression of the higher mortality of females in the earlier stages, and do not furnish any substantiation of such a notion.

There still remains the possibility of a difference in the death rate of the two sexes after reaching what we have called adult life, and this will be examined next. This group, it will be recalled, includes 749 birds which attained the age of six months or more. Of these 125 died from "natural" causes, 391 were alive on December 1, 1914, and 233 were killed, sold, or otherwise disposed of at periods presumably shorter than would have been their natural space of life. Table II summarizes the data for the first two classes—those which died natural deaths and those which were alive at the time of compilation. These two classes together represent a total of 516 birds, the *females* being considerably in excess. The numbers are, 244 males and 272 females. For purposes of tabulation they have been divided into periods of 1 year, except the first group, which is only a six-month period, including birds between six months and one year of age.

TABLE II.—*Adult birds alive and which have died at specified ages.*

AGE.	6 mos.–1 yr.		1 yr.–2 yrs.		2 yrs.–3 yrs.		3 yrs.–4 yrs.		4 yrs.–5 yrs.		5 yrs.–6 yrs.		6 yrs.–7 yrs.		7 yrs.–8 yrs.		Totals.	
SEX.	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Total reaching given age	244	272	229	248	210	214	206	203	201	199	200	195	198	194	197	194	……	……
No. which died at given age	15	24	19	34	4	11	5	4	1	4	2	1	1	0	0	0	47	78
Alive December 1, 1914	1	0	23	31	81	88	65	55	13	11	8	6	2	1	4	2	197	194
Totals	16	24	42	65	85	99	70	59	14	15	10	7	3	1	4	2	244	272
Per cent. dead of total reaching given age	6.1	8.8	8.3	13.7	1.9	5.1	2.4	2.0	0.5	2.0	1.0	0.5	0.5	0.0	0.0	0.0	……	……

Perhaps the most striking fact noticeable in this table is that from the age of six months to three years the number of females which died is strikingly in excess of the males. To a less extent the same is true (except in the six-month group)* of the number of females alive on December 1, 1914, as compared with the males. Beyond this age the numbers dead are so small that they have little meaning; it will be observed, however, that in the case of the birds alive at ages above three years the earlier condition is reversed, there being more males than females alive at each age above three years. The total number of female deaths in the adult period is greatly in excess of the male deaths, there being 78 of the former recorded and only 47 of the latter. By far the greater number of these occurred under the age of two years. At the bottom of the table the number of deaths for each sex is given as a percentage of the total number of birds which reached that age, the sexes again being considered separately. These show that the highest percentage of the females died between the ages of one and two years, and in each group up to three years the percentage of females which died is considerably greater than of males; beyond this point the figures are scarcely significant.

Considering the birds alive, it will be seen that there are somewhat more one-and two-year-old females than males; but of the older ages the males are always in excess, so that the total number of males slightly exceeds the females, being 197 as against 194, a ratio (101.6: 100) distinctly lower than the normal ratio at hatching.

Summarizing the results of Table II, they seem to show that there is a high mortality of both sexes during the first two or three years of their adult life, but that it is especially high in the females between the ages of one and two years. The difference between the percentage of female and male deaths is considerably greater at this age than at any other and it seems not unlikely that this may be associated with trouble connected with the onset of ovulation. This greater mortality of females in the early adult ages, together with the somewhat

*Living birds hatched before June in 1914, and consequently over six months old on December 1, are not included, since their sexes are undetermined. The one male less than one year old at this date was hatched in December, 1913.

greater number of males hatched, may account for the prevailing impression of the considerably greater proportion of males among adult pigeons. It may be recalled, however, that in the total number of pigeons reaching adult age (Period D; see Table I) there was a preponderance of males even beyond that at hatching and it is natural to ask what has become of these. If we turn to the 233 birds "killed, sold or otherwise disposed of" after reaching six months of age we obtain considerable light on this point, for only 89 of them were females and 144 were males. In other words, we have practically equalized the effects of the greater mortality of females by a selection favoring males in eliminating birds from the flock.

There seems then to be real substantiation for the idea that male pigeons are commonly in actual excess in adult populations. The impression of an excess of males may, moreover, be accentuated by certain facts in their behavior. The male birds display their sexual characteristics, as a rule, at a considerably younger age than do the females. Sexual behavior is, however, far from an invariable criterion of sex in young birds; while it presents itself in a positive way in many young cocks—by cooing, strutting and fighting—it is largely negative in the hens and in the less aggressive or backward cocks. As a consequence the breeder soon comes to recognize a considerable number of his young males, while the remainder of the young stock remains as an undetermined residuum. The males are thus more conspicuous, and in this way an impression may be gained of a larger proportion of them than actually exists.

It should be emphasized again in this connection that the data here presented pertain only to our own flock. It is possible that different results may obtain under different conditions. We believe, however, that our conditions are fairly representative in most respects, and that the conclusion here reached may be capable of general application.

The Ratio of Bisexual to Unisexual Broods and the Relation of Sex to the Order of Laying of the Eggs.

Domestic pigeons ordinarily lay two eggs at each nesting, and it is another prevalent notion among pigeon breeders that these always, or at least in a majority of instances, give rise to a pair of squabs, that is, to one of each sex. Furthermore, it is commonly maintained that the first egg of the two laid produces a male, while a female is hatched from the second egg of the clutch. This belief is not only firmly established now, but goes far back into antiquity, for Aristotle (1910, 562[b]) has the following to say on the subject. "Birds of the pigeon kind, such as the ring-dove and the turtle-dove, lay two eggs at a time; that is to say, they do as a general rule, and they never lay more than three." "The hen-pigeon, as has been said, occasionally lays three eggs, but it never rears more than two chicks, and sometimes rears only one; and the odd one is always a wind-egg."* "The pigeon, as a rule, lays a male egg and a female egg, and generally lays the male egg first; after laying it allows a day's interval to ensue and then lays the second egg."

A point as interesting as this could scarcely be expected to escape Darwin, and indeed in connection with his statements previously referred to (Darwin, 1875, p. 247) he has the following to say on this matter: "Usually the two birds reared from the two eggs laid in the same nest are a male and a female; but Mr. Harrison Weir, who has been so large a breeder, says that he has often bred two cocks from the same nest, and seldom two hens." Little serious attention appears to have been given to settling the matter, however, until it was taken up by Cuénot. This author first gives the subject considerable attention in a general paper on the determination of sex in animals (Cuénot, 1899) and reviews the literature up to his time. Most of his references have been inaccessible to us, but for the sake of completeness we include a summary of the observations and the citations to the original sources as given by him.

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*The term "wind-egg" was formerly applied loosely to any imperfect, soft-shelled, unimpregnated or addled egg; its use is now obsolete.

Flourens (1864), in eleven broods found in each case a male and a female; Bailly-Maitre, cited by Giard (1897), while admitting that each clutch generally gives a male and a female, reports a pair of common Mondains which three times in succession gave two males in each brood; neither did De Brisay, also cited by Giard (1897), admit this as a general rule, for he had a pair of "Pigeons satin" which in six years produced some half-hundred young, of which only two were females, and a pair of "Colombes diamant," which of 13 young produced a large majority of females. Similarly, Thauziès, a breeder of homing pigeons, cited by H. De Varigny (1898), considers it rather rare that the two young are of different sexes, and reports that in 7 nestings two males were obtained 5 times, two females once, and a male and a female only once; one pair of birds produced nothing but males during three consecutive years. Remy Saint-Loup (1898), raised two Ring-doves* captured in the same nest and both proved to be males.

Cuénot's own observations at that time were not extensive; he reports having examined 9 broods,† after assuring himself with great care that the two eggs came from the same mother, and of these he found that 2 gave both males, 2 gave both females, and in 5 cases there was a male and a female. Cuénot concludes that while it is certain that the young from the two eggs laid at a time by a pigeon are frequently a male and a female, it is no less certain that they are often of the same sex; in view of the conflicting data he suggests that the proportion of bisexual and unisexual broods may vary in the different races and sub-races of pigeons.

As to the order of the sexes in the bisexual broods, Cuénot states that Flourens (1864), reported the first-laid a male in each of the eleven cases examined by him. Cuénot himself presents the results of three observations, in each of which also he found the squab from the first egg was a male, while that from the second was a female; he was unable, however, to note any constant relation of sex to the weight or shape of the egg.

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*Presumably *Columba palumbus;* not *Turtur* (*Streptopelia*) *risorius.*

†Cuénot says he examined "8 pontes" but they sum up to 9, as indicated above.

In a later paper Cuénot (1900), presents much fuller data. He reports 65 broods of homing pigeons in all of which he made certain that both eggs were from the same female. The results were: 17 broods, both males; 14 broods, both females; 34 broods, a male and a female. By chance, as, for example, by tossing two coins, the expectation for 64 throws would be two heads 16 times, two tails 16 times and a head and a tail 32 times. He points out, however, that we must take into account that there were 68 males and only 62 females; correcting for this, chance distribution gives the expectation of both males 17.7 times, both females 14.7 times, and one of each 32.4 times, which is almost exactly the result obtained. It is therefore necessary he concludes, to abandon the fallacy of the bisexuality of the broods, beyond what would be expected from chance.

Further observations caused him to alter also his earlier conclusion as to the proportion of cases in which the first egg produces a male. The first egg was marked before the second was laid in 30 cases, and both squabs were dissected two days before they were due to hatch. In 15 of the cases the first egg produced a male, and in the other 15 cases a female. It appears also, therefore, to be a matter of chance whether the first egg laid is male or female. Cuénot thinks it probable that Flourens did not make his observations himself, but trusted to a subordinate.

At the time we began our observations we were unaware of Cuénot's work. While the popular notions seemed *a priori* extremely improbable, if they were true they presented some very interesting and important theoretical as well as practical problems, and it seemed advisable to accumulate as many data on this phase of the pigeon work as could be done consistently with the studies on inheritance.

If it should prove true that there is a constant relation between the order of the laying of the eggs and the sex of the squabs hatched from them, or indeed if there should be a greater tendency in this direction than could be accounted for by chance, it would be necessary to abandon, or materially to modify, the theory which seems generally so well established, that sex is irrevocably determined by chance

at the time of fertilization of the egg. Furthermore, it is difficult
to conceive by what sort of mechanism a relationship of this sort
could be effected, especially when we consider the irregularities which
may occur in the egg laying of the pigeon. While it is true that they
ordinarily lay two eggs at each nesting, it is not at all uncommon among
domestic pigeons for the hen to lay only one, especially towards the
beginning or end of the season; and there are occasionally females
which seldom or never lay more than one egg at a sitting. On the
other hand, according to various authors (see, for example, quotation
from Aristotle, p 478) they may occasionally lay three or even four
(Wright, 1879, p. 33). Tegetmeier (1868, p. 10) asserts, however,
that they never lay more than two eggs in a nest "unless, from the
absence of a sufficient number of male birds, two hens pair and make
a nest, when four are laid, which of course are sterile, and after being
sat upon for the usual period are deserted." We have had cases of
three eggs, but none in which we could be absolutely certain that the
third egg was laid by the same bird, though the cicumstantial evidence
to that effect was strong. In at least one case the third egg hatched
normally.

Certain birds, at least, that normally lay clutches consisting of
a considerable number of eggs, may be induced to continue laying
for a longer or shorter time if the eggs are removed as laid. This
is the case with most of our domestic poultry, such as the ordinary
hen, duck, goose, turkey, and so on. The classical example of a non-
domesticated bird which has often been made to produce an unusual
number of eggs in this way is the Flicker (*Colaptes auratus*). The
usual clutch of the Flicker is from 6 to 9 eggs, but much larger
numbers may be obtained if the eggs, or all but a "nest egg," are
removed as laid, the largest record being of 71 eggs laid in 73 days,
beginning about May 6th. Burns (1900, p. 45) has given a summary
of such cases for the Flicker, and also for a number of other wild
birds. With pigeons, however, removal of the first egg is ineffective
in inducing the female to lay any more than two at a time; nor
have we yet found any method by which this result may be brought

about. The only experiments on wild species which normally lay a restricted number that we have found mentioned are some tests which Levick (1914, p. 127) made in the Antarctic with McCormick's Skua (*Megalestris maccormicki*). As in the pigeon the normal complement of this gull is only two eggs. Levick says: "In order to find out how many eggs a Skua would lay, I marked some nests, and took the eggs as they were laid. In each case a second egg was laid, but when this was taken no more appeared. In two nests I removed the first egg as soon as it was laid, but left the second, which was then sat upon by the parent, who was content with it, or unable to lay a third." It would appear that in birds which normally lay so few eggs at a time, the stimulus for further production caused by removing the eggs, does not occur early enough to allow for continuous production.

Considering the matter from a genetic or phylogenetic standpoint, it would be surprising if a definite relationship of sex to the two eggs of the set were to have become established in one group of pigeons and not in all. This can hardly be the case, however, for while two is the usual number there is apparently no uniformity in this respect in different members of the family Columbidae, or even within the genus Columba. The Red-billed Pigeon (*Columba flavirostris*), for example, is reported to lay but a single egg at each nesting; the Passenger Pigeon (*Ectopistes migratorius*), formerly so abundant in North America, but now extinct, ordinarily laid but a single egg, but sometimes laid two; the Blue-headed Quail-dove (*Starnoenas cyanocephala*) lays one or two; while it is stated that the Mourning Dove (*Zenaidura macroura*) may even lay three or four (Davie, 1889, p. 157). Inglis (1899) reports the laying of three eggs in a nest by a Bengal Green Pigeon (*C. phoenicopterus*). These records are from nests taken in the open, so of course the possibility of the extra eggs having been laid by a different female cannot be entirely excluded.

The relation which the popularly assumed facts, if true, might bear to practical pigeon breeding is illustrated by directions which appeared in a pigeon paper a few years ago for enabling the breeder to maintain

an equality of sexes in his breeding stock. The same general idea is fairly current, and appears from time to time in the pigeon magazines. The article referred to first stated that the difficulty the breeder commonly experiences is that at the beginning of the breeding season he finds he has an excess of males in the stock he has saved for breeding. If this difference is very great it may mean considerable loss to a breeder raising squabs for market on a large scale. To avoid this difficulty the author made suggestions of procedure based on certain definite assumptions, somewhat as follows: (a) A pair of squabs, that is a male and a female, is hatched from each complement of two eggs; (b) the first egg laid produces the male, the second egg gives rise to the female; (c) the first egg being laid a considerable time in advance of the second, hatches first, and therefore (d) the time of incubation being the same for both eggs, it follows that (e) the first squab to hatch is a male, while the female hatches sometime later; (f) as a consequence of being hatched earlier the male gets a start in growth over the female, and consequently (g) the larger squab of a brood is a male and the smaller a female. From these assumptions the conclusion was drawn that in order to obtain an equal number of males and females all the breeder need do would be to separate the two members of each brood while he still knew which they were, putting the larger squab in each case into one pen and the smaller into another. He would then have one pen of males and the other of females and he could choose from them to suit his convenience.

Directions depending upon much the same assumptions are given by Wright (1879, p. 33). Speaking of the two eggs of a set he says, "These two are in three cases out of four a cock and a hen, but by no means always so, as usually supposed; about twenty-five per cent. being pairs of one sex or the other. When one is a hen it is generally the last of the two, and as such likely to be stunted in growth from the earlier hatching of the first, which has had a start by the hen standing over it before the other was laid, and thus gets fed and becomes larger and stronger before the hen is hatched. To avoid this, laying should be watched for every evening, and the first egg taken away

and replaced by a nest egg of bone or a waste pigeon's egg, to be replaced the evening the second is laid. This plan will save or improve many a hen that otherwise would be dwarfed in rearing." No figures are advanced in substantiation of the statements made.

Assumptions (*a*) and (*b*) have both been disproven by the observations of Cuénot (1900), and our results support his. Our general conclusions were published in abstract several years ago (Cole, 1911); since then we have added many more corroborative data, all of which are presented below. Assumptions (*c*), (*d*) and (*e*) are considered in a later section; data bearing on (*f*) and (*g*) have already been presented. Briefly, it may be said that none of these assumptions is true in its entirety; some are partially true, while others have no foundation whatever in fact. It will be noted that among these no mention is made of an excess of males hatched, one fact helping to explain their reputed excess in the breeders' lofts which appears to be well established.

Our data showing the relation of sex to order of laying of the eggs, summarized to July 18, 1914, are presented in Table III.

Table III.—*Sex of squabs in relation to order of laying of eggs.*

First Egg:	A♂	A♀	A♂	A♀	A♂	A♀	A-	A-	X(Y)♂	X(Y)♂	X(Y)♀	X(Y)♂	X(Y)♀	A♂	A♀		
Second Egg:	B♀	B♂	B♂	B♀	B-	B-	B♂	B♀	X(Y)♀	X(Y)♂	X(Y)♀	X(Y)-	X(Y)-	-	-	Totals.	Row.
Records																	
1 Rhode Island	41	41	43	55	36	39	50	19	13	7	4	4	5	7	2	366	1
2 Wisconsin	6	7			44	32	42	37	176	99	94	64	63	16	16	696	2
Totals																	
3 Broods	47	48	43	55	80	71	92	56	189	106	98	68	68	23	18	1,062	3
4 Individuals	94	96	86	110	80	71	92	56	378	212	196	68	68	23	18	1,648	4
5 Males	47	48	86		80		92		189	212		68		23		845	5
6 Females	47	48		110		71		56	189		196		68		18	803	6
7 A males	47		43		80					106				23		299	7
8 A females		48		55		71					98				18	290	8
9 B males		48	43				92			106						289	9
10 B females	47			55				56			98					256	10
11 ♂♀ or ♂♂ broods	47	48							189							284	11
12 ♂♂ or ♀♀ broods			43	55						106	98					302	12
13 ♂♂ broods			43							106						149	13
14 ♀♀ broods				55							98					153	14
15 ♂♂ { In broods in which sex of	47	48	86						189	212						582	15
16 ♀♀ { both squabs (was determined)	47	48		110					189		196					590	16

This table contains also other records of known sexes, thus giving the complete total of sexes determined to that date, but the ratio obtained from these numbers has already been discussed on (p. 465). The first egg laid is designated the "A" egg, while the second is egg "B;" similarly the squabs from the two eggs are designated "A" and "B" according to the respective eggs from which they hatched. In case both eggs were laid before they were found, so that the order of laying was unknown, or if it was not determined which squab hatched from which egg, they are referred to as eggs "X" and "Y" or squabs "X" and "Y" to designate this fact. It is a part of the daily routine to mark the newly laid eggs. In the work at the Rhode Island Station one of the eggs was removed to the incubator a day or so before it was due to hatch; the squab hatching from it was marked by a thread tied loosely around the leg, and was then returned to the nest. The thread was removed when the permanent legband was put on at the age of 10 to 15 days.*

The first four columns of Table III record the cases in which the sex of both A and B are known; in the next four columns only one, either A or B, is known, the other egg having been sterile, accidently broken, or the sex for some other reason indeterminable. In the following three columns the sex of both squabs is known, but not the order of laying of the eggs, or else it is not known from which egg a particular squab came. The following two columns show the sex of only one of the squabs under similar conditions; and finally in the last two columns are those cases in which but a single egg was laid, it being designated "A" accordingly.

The results of interest in the present connection are shown in the combined summaries in the rows in the lower part of the table. Rows 5 and 6 show a total of 845 males to 803 females, or a ratio of 105 : 100, which we have considered as normal. By comparing

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*A much simpler method of marking young squabs for identification purposes is now employed. With scissors the claw of any desired toe may be clipped off on young squabs, without bleeding, and without causing the bird any apparent pain. If clipped back beyond the growing region this gives a permanent mark by which the bird may be identified through life. We depend upon it, of course, only until the permanent band is put on.

rows 7 and 8, in which the proportion of total males to total females is nearly 108 : 100, we find that of the 589 known A-eggs, 299 produced males and 290 females. This is a ratio of only 103 : 100; in other words, *the excess of males from A-eggs is slightly less in this case than normal for both eggs.* As would be expected, we find a correspondingly larger proportion of males to females from B-eggs, namely 289 males to 256 females (rows 9 and 10), or 113 : 100. This result confirms that which Cuénot obtained with small numbers, to the effect that there is no basis in fact for the belief that the A-egg more often produces males and the B-egg females.

Considering now only those cases in which the sexes of both squabs were determined, we note (rows 11 and 12) that there were 284 bisexual broods to 302 unisexual, and that of the latter 149 consisted of two males and 153 of two females (rows 13 and 14). The expectation, if we assume that sex is determined by chance, would be equality in both instances. In the ratio of bisexual to unisexual broods the chances are about even that the divergence from equality would be as great as 'that observed, with the odds very slightly against it.* On the other hand the ratio of 149 broods 'both males' to 153 broods 'both females' is well within expectation.† While, therefore, the numbers of the bisexual and unisexual broods are rather divergent, they are not so far apart as to demand any other explanation than that of a chance result, and for practical purposes the male as compared with the female broods may be considered as equal. It happens that there are four more of the latter than of the

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*Ratio obtained, 284 : 302.

Deviation from equality $= 9$.

Probable error ($0.67449 \sqrt{n\,p\,q}$; n, number of individuals, p and q, proportions expected in each class, in this case $\frac{1}{2}$ in each) $= 8.1638$.

$\dfrac{\text{Deviation}}{\text{Probable error}} = 1.1.$ The odds against a deviation as great as 9 are accordingly 1.18 to 1 (Pearl and Miner, 1914).

†Ratio obtained $= 149 : 153$.

Deviation $= 2$.

P. E. $= 5.86$.

$\dfrac{\text{D}}{\text{P. E.}} = 0.34.$

former, and therefore the total number of females in the broods in which the sex of both squabs was determined exceeds the total number of males by 8 (rows 15 and 16). This difference, of course, cannot be taken as having any significance.

Time of Laying of Eggs A and B.

That a day intervenes between the laying of the two eggs is a fact known by all breeders of pigeons, but no accurate study of the time of laying appears to have been made. The statement by Wright is more definite in this respect than most. He says (Wright, 1879, p. 33): "Soon after matching—generally ranging from one to three weeks, according to age and time of year—the cock will begin to drive the hen towards her nest, and seem uneasy whenever she is away from it. That is a sign laying is near, and in fact the eggs generally appear in from two to five days after. Two are laid; the first usually about five or six o'clock in the afternoon, the hen standing more or less over it all the next day and night, and laying the second egg about two o'clock on the third day."

During the first eighteen months of our work an attempt was made to obtain as accurate records as possible of the time of laying and of hatching of the eggs. A routine was established of making hourly observations from 7 A. M. to 8 P. M., and this was adhered to as far as conditions permitted. As a result we have records of 101 sets of eggs, the time of laying of each of which is known within the limits of one hour; 12 of these records are scattered through 1907, while the remaining 89 were made during the months of January to July, inclusive, in 1908. In many cases the time of laying is known more closely than the limit here ascribed, but for statistical treatment the records have been grouped into one-hour classes, the mid-value of the class being the half hour. Such records as fall exactly on the even hour have been uniformly placed in the class preceding that hour; for example, an egg recorded as laid at 4 P. M. has been classed as 3—4 P. M. We have many other records in which the time of laying is known within a somewhat longer period than one hour, but such records have not been included in the present discussion.

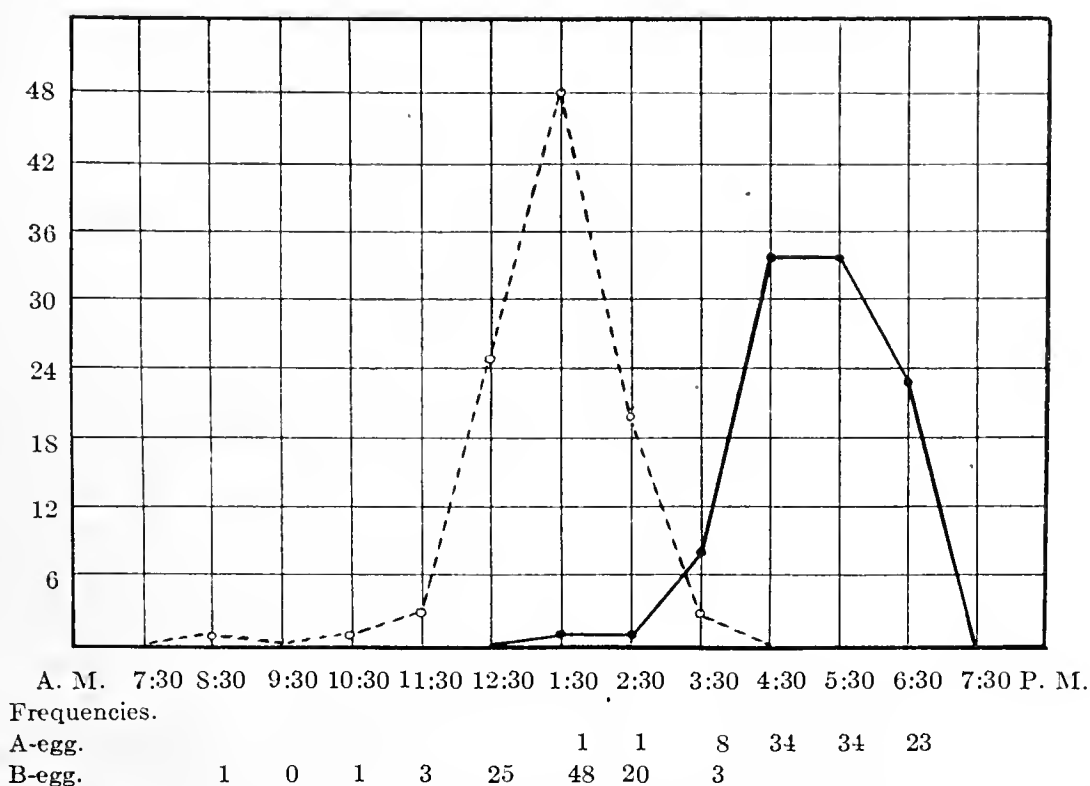| Frequencies.	A. M.	7:30	8:30	9:30	10:30	11:30	12:30	1:30	2:30	3:30	4:30	5:30	6:30	7:30 P. M.
A-egg.									1	1	8	34	34	23
B-egg.			1	0	1	3	25	48	20	3				

FIG. 2. Curves showing time of day the two eggs were laid in 101 sets; solid line, first egg; dotted line, second egg, on second day following first.

The distribution of frequencies with respect to the time of laying of both eggs is shown in Figure 2. The unbroken line represents the data for the first egg, the broken line for the second; but it must be remembered that although for convenience of comparison the two curves are here superimposed, in reality egg B is laid on the second day following egg A, and that therefore there is a period of nearly 48 hours between the two curves. The frequencies for the respective classes are given below the figure. Basing our statements entirely on the data here presented, we may draw the following conclusions:

1.   Egg A is always laid in the afternoon, some time between the hours of one and seven.

2.   Egg A is most frequently laid from four to six in the afternoon; the mean time is 5:10 P. M.

3.   Egg B is usually laid early in the afternoon, most frequently between one and two o'clock, but may be laid as early as 8 to 9 A. M., and as late as 3 to 4 P. M.

4.   The mean time of laying of egg B is 1:22 P. M.

5.   The mean time between the laying of eggs A and B is accordingly 44.21 hours, or 44 hours, 12 minutes.

6.   From the shape of the curves it might be inferred that there is somewhat greater variability in the time of laying of A than of B, although the range of the latter is slightly greater. A comparison of the standard deviations in the two cases, however, shows no significant difference. These are: for A, 1.008 $\pm$ 0.048 hours; for B, 1.002 $\pm$ 0.048 hours.

As stated above, the mean time intervening between the laying of eggs A and B is 44 hours and 12 minutes; the extremes are 42 hours on the one hand and 47 hours on the other. The distribution of frequencies with respect to interval between layings is shown in Figure 3. The variability of this interval as measured by the

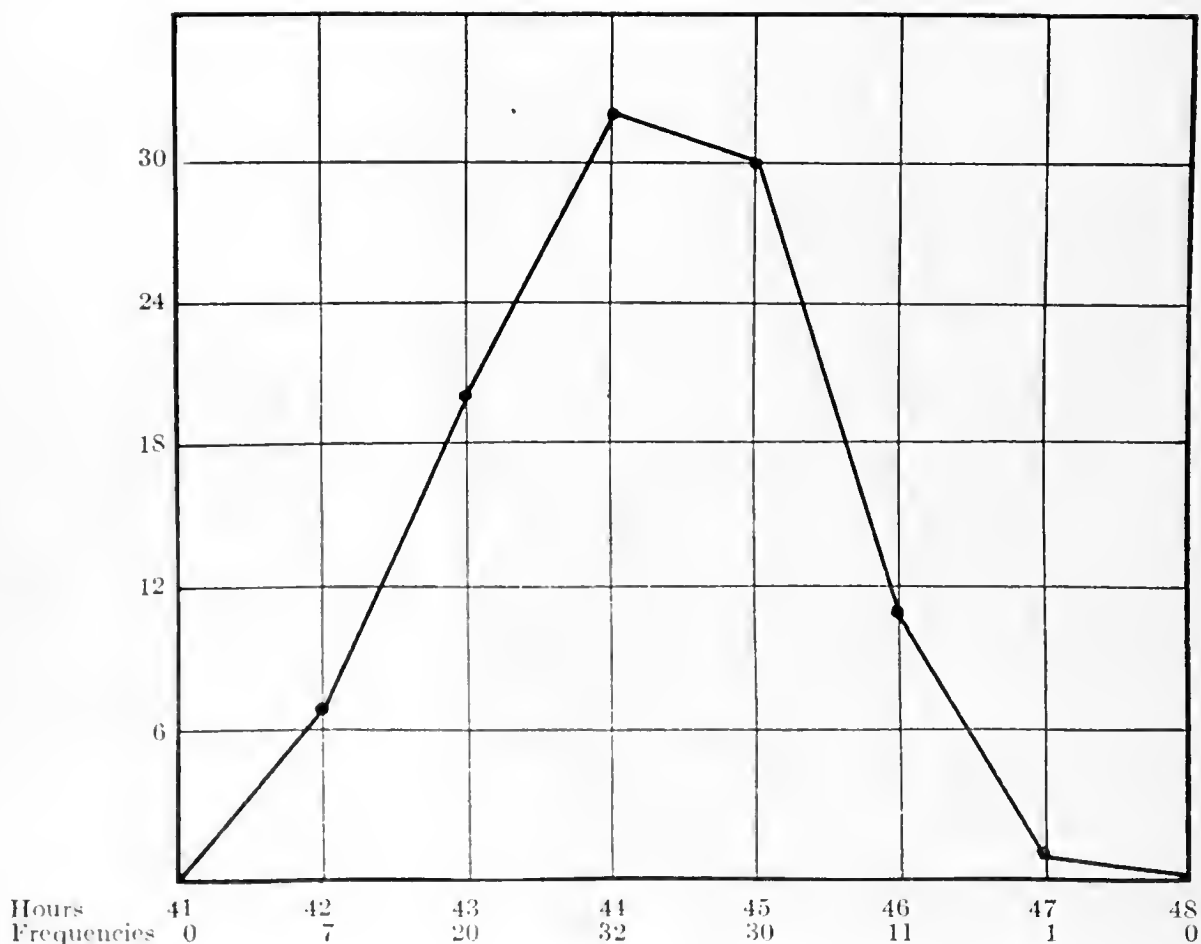| Hours	41	42	43	44	45	46	47	48
Frequencies	0	7	20	32	30	11	1	0

FIG. 3.   Curve showing interval in hours between laying of first and second eggs in 101 sets.

standard deviation is slightly, though scarcely significantly, greater than the variability in the times of laying of A and B respectively ($\sigma = 1.120 \pm 0.079$).

TABLE IV.—*Interval between laying of eggs A and B arranged by months.* (*Includes 89 records made in 1898.*)

MONTH.	Hours between laying of A and B.						Total.	Mean.
	42	43	44	45	46	47		
January.	....	....	....	1	....	....	1	45.00
February.	....	....	1	4	3	1	9	45.44
March.	1	2	4	5	4	....	16	44.56
April.	....	4	8	7	3	....	22	44.41
May.	....	4	4	9	1	....	18	44.39
June.	1	5	6	1	....	....	13	43.54
July.	2	2	6	....	....	....	10	43.40
Total.	4	17	29	27	11	1	89	44.30

Perhaps the most interesting fact with respect to the interval between the laying of A and B comes out when the records are considered by months, as is done in Table IV. The 12 records of 1907, which were scattered throughout the year, are not included in this table. A comparison of the means for the different months shows that with the exception of January, for which there was but a single record, and which may therefore be disregarded, the mean time between the laying of A and B decreases perceptibly for each month from February to July. This fact is shown more graphically in Figure 4, where the means are plotted with their values as ordinates and the months as abscissæ. The straight line which best fits these observations has the equation $y = 46.02 - 0.385x$, where y is the interval between the eggs in hours and x the month of the year from February to July, inclusive.
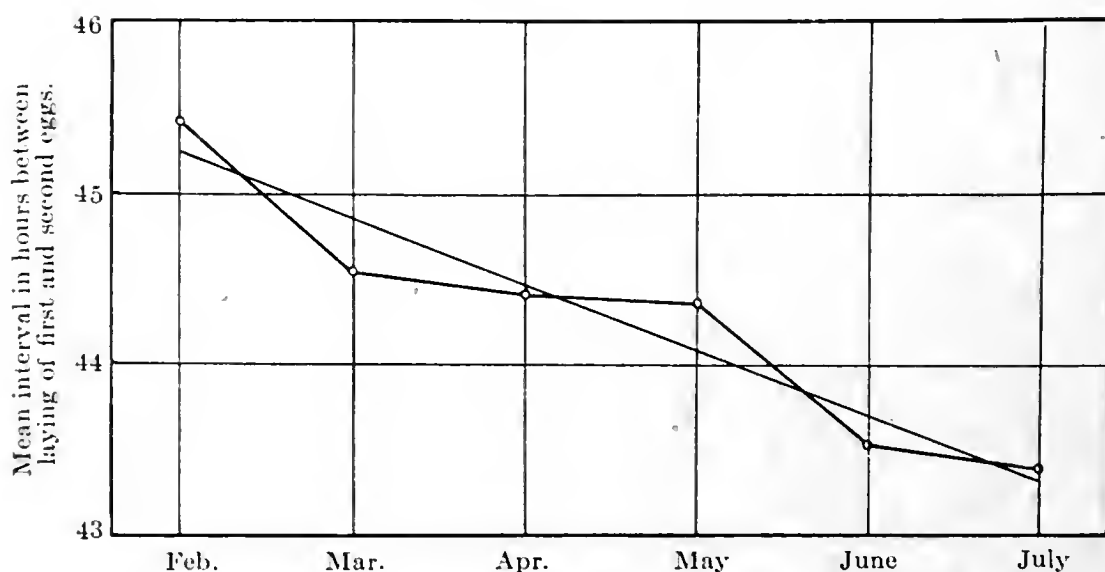
FIG. 4. Decrease in monthly mean interval between laying of the two eggs of a set, from February to July, 1908, inclusive.

It is unfortunate that records were not obtained for the remaining months of the year so that we might know whether the interval would continue to decrease or whether it would shorten again as the season progressed. The latter seems the more probable assumption, but in the absence of further records there is nothing to test it. Two possible explanations suggest themselves to account for the pro-gressive shortening of the mean interval between laying of A and B from February to July. In the first place it is possible that this change is simply a reaction to temperature conditions, the physiological processes of the bird being accelerated and the interval correspondingly shortened in response to the warmer weather as the season advances. It seems rather more probable, however, that the physiological change in ovulating activity is directly related to the normal cycle of egg production in the pigeon. In domesticated pigeons the cycle of egg production undoubtedly extends over a longer period than it does in the wild state, as is the case also in the domestic fowl. Whether, in pigeons, this is a result of selection, direct or indirect, we do not know. At any rate the normal season of egg production may be assumed as in the spring or early summer. With the extension of the season we might expect the highest activity of the physiological processes of egg production to occur at the normal

season, and a lessened activity at the beginning of the season, leading up to the maximum.

If a female which laid one of the earliest A-eggs (1-2 P. M.) had laid the second egg among the latest of those recorded (3-4 P. M.) the interval would have been 50 hours; on the other hand the shortest possible interval (A, 6-7 P. M.; B, 8-9 A. M.) by the same method of calculation would have been 38 hours. As a matter of fact we have seen (Fig. 3) that the shortest interval between the laying of A and B was 42 hours and the longest 47 hours. This suggests a distinct positive correlation between the time of laying of A and B, and in Table V the data are displayed in the form of a correlation table.

TABLE V.—*Correlation between times of laying of first and second eggs.*

		Time of laying second egg.								
		7:30– 8:30.	8:30– 9:30.	9:30–10:30.	10:30–11:30.	11:30–12:30.	12:30– 1:30.	1:30– 2:30.	2:30– 3:30.	Totals.
Time of laying of first egg.	12:30—1:30	....	....	1	....	....	....	....	....	1
	1:30—2:30	1	....	....	....	....	....	....	....	1
	2:30—3:30	....	....	....	1	3	3	1	....	8
	3:30—4:30	....	....	....	1	8	20	5	....	34
	4:30—5:30	....	....	....	1	9	15	6	3	34
	5:30—6:30	....	....	....	....	5	10	8	....	23
	Totals	1	0	1	3	25	48	20	3	101

The distribution of the records in the table indicates some correlation, and the calculated coefficient gives $r = + 0.38 \pm 0.057$, which is a very sensible correlation. The equation to the regression straight line is $y = -0.48 + 0.378x$, where x is the time P. M. of laying of the first egg, and y that of the second. By substituting in the formula the time that any given first egg is laid, the value of y gives the most

probable time of laying of the second egg. This formula is based on all the available data, and is not corrected for the different months.

For convenience of reference the more important constants which have been developed in the foregoing section are here brought together.

Mean time of laying of A.......................5:10 P. M.
Mean time of laying of B (on second day following A) 1:22 P. M.
Standard deviation of time of laying of A . . 1.008 $\pm$ 0.048 hours.
Standard deviation of time of laying of B . . 1.002 $\pm$ 0.048 hours.
Mean interval between laying of A and B..........44.21 hours.
Standard deviation of same..............1.120 $\pm$ 0.079 hours.
Coefficient of correlation of laying of A and B......0.38 $\pm$ 0.057.
Regression straight line of same..........$y = -0.48 + 0.378x$.

Time of Hatching of Eggs A and B.

Aristotle (1910, 562^b30) gives the period of incubation of the pigeon as only 14 days, but it would seem as if he must here be referring to one of the smaller species, such as the Turtle Dove. Moore (1735, p. 11) in his famous "Columbarium" says: "The time of a pigeon's incubation, which trouble is equally divided between the cock and hen, except that the hen always sits all night, is nineteen or twenty days from the first egg, and seventeen or eighteen from the last," with which statement, as regards the period of incubation, modern authorities are in accord.

Our books at the present time contain several thousand records of the day of laying and the day of hatching of eggs, taken in the course of the regular daily routine. Since, however, the recording has not always been done at the same time of day, the period of accuracy may in reality sometimes be longer than a 24-hour period, as for example would be the case if the records were taken in the forenoon of one day, and not again until the afternoon of the day following. We have, however, 118 records in which the time of hatching of both eggs is known within a 12-hour period; for those which hatched in the daytime the time of incubation of the egg is indeed often known

within an hour or two, but for the night we seldom known the actual time of hatching closer than that it occurred between 6 or 8 P. M. and 8 A. M. It seems best therefore simply to group the hatchings into half-day classes, the one including the daytime period from 8 A. M. to 8 P. M., the other the nighttime from 8 P. M. to 8 o'clock the following morning.* By this method an egg hatching between 8 o'clock in the morning and 8 o'clock in the evening of the seventeenth day after the laying of egg B would be put in class "17;" if it was not hatched by 8 P. M., but was found out of the shell at 8 o'clock the next morning (that is, on the eighteenth day) it would be put into the "17.5" class. As has already been stated (p. 486) one of the eggs was often put into the incubator a short time before hatching, and hatched there, but there is no reason to believe that this has had an appreciable effect on the results.

Days.	14.5	15	15.5	16	16.5	17	17.5	18	18.5	19	19.5	20	20.5
A-egg.	1	2	20	25	39	16	10	1	3	1			
B-egg.			5	4	45	38	20	2	1	1	1	0	1
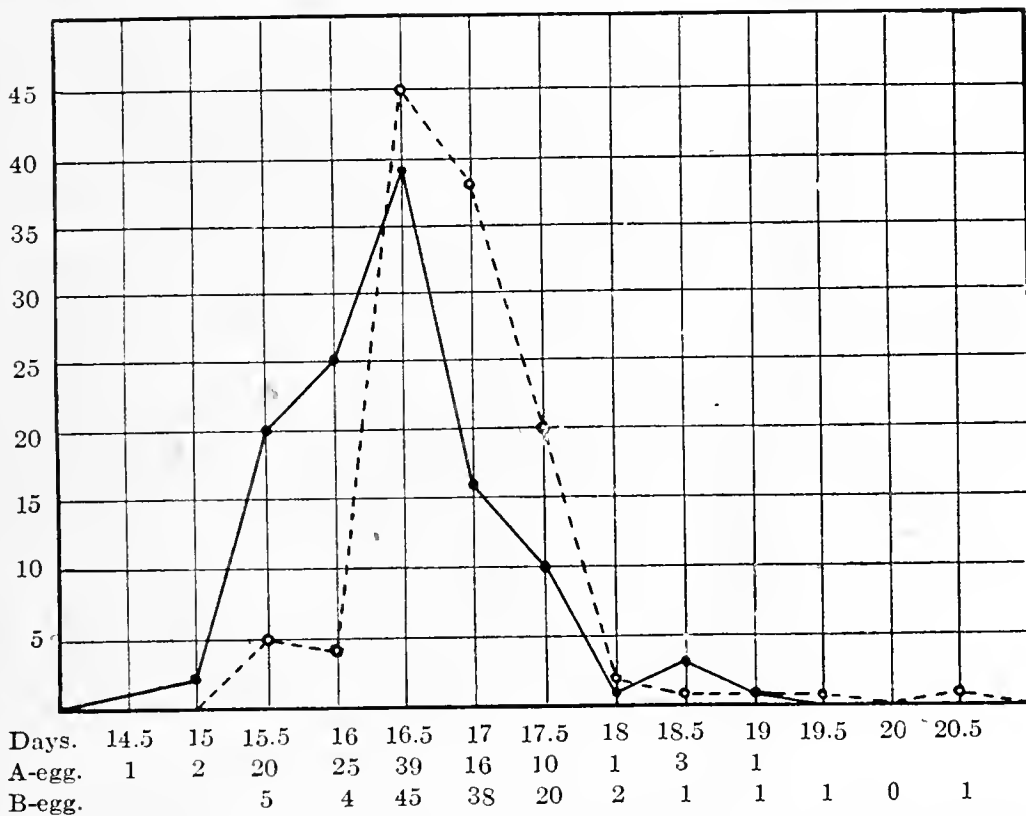
FIG. 5. Curves showing the time of hatching of the first and second eggs, in days after the laying of the second egg. Solid line, first egg; dotted line, second egg.

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*As a matter of fact observations in many cases were not made after 6 P. M. Tabulations on this basis and on the 8 to 8 basis, show however practically no difference so far as our records indicate and it has accordingly seemed best to make the two classes of equal length. It should be remembered, however, that in an unknown proportion of the cases the night period is in reality longer than the day period. This may account in part for the larger number of recorded hatchings at night (see p. 497).

The distribution of frequencies with respect to time of hatching of both eggs is shown in Figure 5, the unbroken line connecting the records for the A-egg and the broken line those for B. The point of greatest interest which immediately impresses one on examining this figure is the remarkable extent to which the two polygons overlap, considering that there is a mean difference of slightly more than 44 hours between the times of laying of the eggs whose hatchings are represented by the two polygons respectively. This fact is further brought out by considering the mean times of hatching of A and B, which, based on the 118 records for each, are 16.42 days for A and 16.89 days for B, the time being reckoned in each case from the day on which B was laid.* In other words, we may say for practical purposes that although there is a mean difference of nearly two days in the laying of A and B, on the average A hatches 18.5 days after it is laid (16.5 days after B) and B hatches 17 days after its is laid.

TABLE VI.—*Correlation between hatching of first and second eggs.*

		Hatching of second egg in days after it was laid.											Totals.
		15½	16	16½	17	17½	18	18½	19	19½	20	20½	
Hatching of first egg in days after laying of second.	14½	1	....	....	....	....	....	....	....	....	....	....	1
	15	1	....	1	....	....	....	....	....	....	....	....	2
	15½	2	2	14	2	....	....	....	....	....	....	....	20
	16	....	1	13	8	3	....	....	....	....	....	....	25
	16½	1	....	17	19	2	....	....	....	....	....	....	39
	17	....	1	....	6	8	1	....	....	....	....	....	16
	17½	....	....	....	3	5	1	....	1	....	....	....	10
	18	....	....	....	....	1	....	....	....	....	....	....	1
	18½	....	....	....	....	1	....	1	....	....	....	1	3
	19	....	....	....	....	....	....	....	....	1	....	....	1
	Totals....	5	4	45	38	20	2	1	1	1	0	1	118

*In addition to the 118 records used above there are 13 in which the time of hatching of A is known, but not that of B, and in 18 cases the time of hatching of B alone is recorded. If these are included the mean for A is not changed, but that for B becomes 16.91.

Furthermore, a high degree of correlation exists between the time of hatching of the two eggs of a set. The data are arranged in the usual fashion in Table VI, and the calculated coefficient gives a correlation of $+ 0.728 \pm 0.029$. The class interval used—i. e., 12 hours—is rather wide, and it is probable that the apparent correlation has been exaggerated somewhat for this reason; that there has, however, been no sensible selection of the data by choosing day and night periods is indicated by a comparison of the means already given with those obtained when the records are treated separately for these periods as is done in Table VII.

TABLE VII.—*Mean time of hatching of eggs A and B after laying of B.*

	Egg A.		Egg B.	
	Number of records.	Mean	Number of records.	Mean.
All records combined....	118	16.42 ± 0.05	118	16.89 ± 0.04
Day hatchings (8 A. M.– 8 P. M.)...........	45	16.42 ± 0.07	45	17.00 ± 0.05
Night hatchings (8 P.M.— 8 A. M.)..........	73	16.42 ± 0.06	73	16.82 ± 0.05

Although there are in both cases more eggs hatched in the night period than in the day* (the numbers happen to be the same for both A and B), the mean is unchanged for A, and in B the difference is not great enough to affect the results of the correlation seriously. We are justified in concluding, therefore, that not only is the mean interval between hatching of all the A eggs as compared with B a half day, but that for any particular set of two eggs there is a strong probability that B will hatch in the next half-day following the

*This may perhaps be accounted for in part by the fact that sometimes the last day records were made at 6 P. M., instead of 8 P. M. (see footnote, p. 495). This does not seem sufficient to account for the entire difference, but we have at present no other explanation to offer for the excess of night hatchings.

hatching of A. The proportion of cases in which A and B hatch in the same half-day is less than half the number of cases in which A hatches before B; in only a small proportion of cases does B hatch before A.   The actual numbers are as follows:

	Number of cases.	Proportion of total.
A hatched before B..................	79	67%
A hatched same half-day as B........................	32	27%
B hatched before A..................	7	6%
Total........................	118	100%

Attention has already been called to the longer period of incubation of A than of B.   Leaving out the fractions, A is laid on the average 44 hours before B, but hatches on the average only 11 hours before B. The difference—33 hours, or almost a day and a half—is the mean time by which the incubation period of A exceeds that of B.   Two possible explanations of this difference between A and B in the time from laying to hatching suggest themselves: (1) Egg A may be physiologically different from B and require a greater amount of incubation, or (2) although there is a longer interval between the deposition and hatching of A the birds may not sit on it so closely when it is first laid, so that it may really receive no more incubation than B.   The first of these suppositions is a very unlikely one from a biological standpoint, for while the possibility of an intrinsic difference between A and B which might influence the time required for incubation, such as gross size, relation of size of yolk to amount of white, or what not, cannot be denied, there are no data to indicate such a relation.   As for the second explanation, there are direct observations in support of it.   Nearly every writer on pigeons states that the birds do not incubate the first egg, but stand over it until the second is laid, when incubation properly begins.   Thus going back to Moore (1735, p. 11) again, we find him stating that "When a

Pigeon has laid her first Egg, she rests one Day between, and on the succeeding Day lays her second: They generally stand over the first Egg, which if you please, you may call an improper Incubation, till the next is laid, and then sit close, that both young ones may be hatch'd at once, or pretty nearly; tho' some will sit close on the first, and by that means hatch one young one two Days before the other." Mr. Kelley states that from his observations he is of the opinion that whereas the hen stands over the first egg in this manner, the cock, when he is on the nest, sits much closer and thus the egg receives some incubation before B is laid. This partial incubation probably accounts for the half-day which A hatches on the average ahead of B. That this is the case is further indicated by the fact that by candling the eggs a day or so after the laying of B the embryo may usually be seen to be in a further stage of development in A than in B, its greater development evidently representing the incubating it has received before B was laid.

Even though we may not be willing to accept the teleological explanation of Moore for the behavior of the female in not incubating the first egg, we must admit nevertheless that it has important biological significance. It is a well established fact for other birds as well as for pigeons that the parents use no judgment in feeding the young, but always fill up first the youngster which is most insistent. In this way it is the most active and vigorous individual which is first satisfied with food. While this may tend toward the survival of the fittest in a brood, it is also an example of failure in biological regulation. It would seem as if it were better, so long as the food supply was sufficient, for the parents' instincts to lead them to feed first the retarded individuals, and thus give all in the brood an equal chance. However this may be, every pigeon raiser knows that where there is much difference in size between the two squabs in a nest, the smaller rarely has much chance of survival unless it is given special attention and care. Disadvantageous difference in size is very frequent in pigeons, and it is our practice to exchange squabs (marked, of course, for identification) in nests of this sort, so as to bring together

those more nearly of a size and thus having more nearly equal opportunities. In this way we undoubtedly save many birds which would otherwise die of starvation or be crowded from the nest by their more fortunate nestmates.

From the foregoing we may conclude then that in all probability the time required for incubation by the two eggs is the same, but although A is laid nearly two full days before B, it receives on the average the equivalent of only about a half-day of incubation before B is laid, so that its mean time of hatching is only a half-day before that of B. From the standpoint of the welfare of the second squab it would probably be better if this interval were still shorter, so that the eggs should hatch essentially at the same time. To this extent the instinct which allows A to be incubated at all in advance of B is imperfect. On the other hand, domesticated birds at any rate often breed during such cold weather that the first egg would freeze if it were not protected at all.

"Control of Sex" in Pigeons.

Practically all of the various factors which have been held by the poultryman to determine sex in poultry, have been put forward for pigeons as well. These include such things as size and shape of egg, position and size of the air space, and the like. Such theories in the past have admittedly had no adequate experimental basis, nor have facts in their support been adduced which could stand the test of scientific proof. More recently, however, certain assertions have been made by Riddle as to the control of sex in pigeons, but the data on which these statements rest have not as yet been published so far as we are aware. Riddle (1914) states definitely and categorically, however, that "By his method of controlling sex in pigeons Whitman showed (1) that the first young of the season (spring and early summer) were nearly all males, and young hatched from the later eggs of the season were nearly all females; (2) that if the two sexes arise from the two eggs of any one clutch, that it is in nearly all cases the first egg which produces the male, and the second egg of the

clutch that produces a female; (3) that birds kept thus mated and overworked at egg-production tend to produce in succeeding years fewer and fewer males before the appearance of females."

Since Professor Whitman's records and notes have never yet been published, but are, we understand, being edited for that purpose by Dr. Riddle, we do not deem it advisable to enter into an extended discussion of these points at this time. Attention should however, be directed again to the fact that Cuénot's results and our own, which combined are of considerable magnitude, are directly contradictory to the second of Riddle's assertions. Furthermore, if his other contentions are true, it is surprising how they are masked when the statistics are treated in their entirety—it seems, indeed, very improbable that the distribution of sexes would balance up so as to give such a decided indication of being chance results as has been shown to be the case in the present report. More attention will be given to this matter in a subsequent paper, in which the data will be considered with respect to the different seasons and conditions.

As one of us has pointed out elsewhere (Cole, 1913) ideas of sex determination are often confused by the pigeon breeder with misunderstood facts of sex-linked inheritance which come up in the course of his breeding operations. Because, for example, he finds that in certain of his matings a large proportion, amounting in some cases to 100 per cent., of the dilute colored offspring (dun, silver or yellow) are females, he concludes that in some way sex is being determined other than by chance. He does not realize that instead of controlling sex he is simply able in certain cases to tell the sex of an individual by its color. In this connection, simply by way of example, a paper by Martin (1912), entitled "How to control the sex of pigeons," may be mentioned.

Length of Time Pigeons will Incubate when Eggs do not Hatch.

It has been claimed by Raspial (1897, 1907) that Turtle doves and pigeons have a very nice adjustment to the normal period of incubation of the eggs, and that if these do not hatch at the proper time the parents will abandon them at once. In his earlier paper he reports the case of a female Turtle dove ["Tourterelle vulgaire (*Turtur auritus*)"] which twice had infertile eggs and abandoned them on the eighteenth day. He argues that since "about 18 days," is the period of incubation of the domestic pigeon, it is probably the same in all of the Columbidae, and this case accordingly proves that the dove "had a very exact notion of the period of incubation and the futility of sitting longer"! As a matter of fact the period of incubation of the Ring dove (*Turtur risorius*) is only about 15 days, and it is probably shorter in all the smaller doves than in the pigeon.

In the second paper he refers again to the Turtle dove and adds the case of a homing pigeon which four times abandoned its eggs on the eighteenth day, the eggs in each case being infertile. He says it is then the knowledge by the female pigeon [Why the female alone, since both sexes take part in incubation?] of the time that should elapse for the eggs to hatch, that enables her to abandon them when they are infertile. Considering the extreme delicacy of the sense which Raspial claims to have shown "enables the Turtle dove to perceive when a profane hand has, during her absence, touched her eggs or young, and which leads to her abandoning them without pity," it is to him "astonishing that she has not the faculty of recognizing sooner that the life is not developed in so intimate a product of her generative organs, and that it is necessary for the whole period of incubation to elapse for her to comprehend the inutility of her efforts." He is furthermore surprised to find this phenomenon in birds of the same family, but living under such different conditions, the one in captivity, the other free. He points out that in contrast to pigeons the domestic fowl has lost this "notion

of the time of incubation," and "will frequently incubate infertile eggs until completely exhausted, if no one takes the trouble to stop her."

Anyone who has had even a little experience raising pigeons well knows that Raspial's generalization with regard to their always abandoning their eggs on the eighteenth day in case they do not hatch is unfounded and unjustified. Wright (1879, p. 40) observes incidentally on this point: "We have *occasionally* kept birds we desired as feeders as much as seven days *on eggs* (in one case eleven days) beyond the proper time of hatching, and then given them young ones only two days old."

Even before we knew of Raspial's papers we had begun the collection of records relating to the time the birds would continue to incubate the eggs in case they did not hatch. Most of the records were made from sets in which the eggs were sterile or in which the embryos died, but in a few cases the eggs were boiled to prevent their hatching, in order that more data on this point might be obtained. In some cases one of the eggs became broken or was otherwise lost during the course of the incubating process; it was then either replaced by a sterile "dummy" egg, or the birds were allowed to continue with the one egg only. In one or two instances one egg hatched, but the squab dying very soon the birds continued incubating the other. Although the records thus represent a variety of conditions, they are all cases in which the birds had incubated normally the full 17 days, and there therefore seems to be sufficient uniformity in the conditions influencing their behavior to allow of their all being treated together as is done in Table VIII. From the footnotes appended to the table it is seen that certain factors, such, for example, as the cases in which no second egg was laid, which might be conceived to have an influence on the time of sitting, are distributed through the records with impartial uniformity.

The 59 matings included in the table are all for the earlier years of our work (1908-1910); since that time the change of method in using foster parents for raising the young of selected parents and the forcing

of the birds to their greatest capacity has not been consistent with obtaining data on the point at issue. We still, however, allow the birds to incubate a day or two beyond the normal period unless it is certain that the embryos are dead, so that from our routine experience together with the data in Table VIII, we are able to state positively

TABLE VIII.—*Length of time eggs were incubated when they did not hatch: counted from time of laying of second egg.*

(The numbers are those of the nestings concerned; each number represents one record.)

Days		17	18	19	20	21	22	23	24	25	26	27	28
	11	.....	.....	.....	.....	.....	.....	755†	.....	.....	.....	.....	.....
	10	.....	.....	.....	.....	.....	.....	688†	.....	.....	.....	.....	.....
	9	.....	.....	.....	.....	.....	.....	558	.....	.....	.....	.....	.....
	8	.....	.....	.....	.....	.....	.....	529	.....	737‖	.....	.....	.....
	7	.....	.....	.....	.....	746	.....	512	.....	716	.....	.....	.....
	6	.....	.....	.....	.....	704	741	505	.....	533	.....	.....	.....
Number of records.	5	.....	.....	.....	.....	445	653	494*	695	464	729	.....	.....
	4	.....	757	.....	.....	425	402‡	475	595†	357	675	.....	.....
	3	605§	477	761	.....	422	400†	426	498	330	674	714	.....
	2	470*†	476	551	386	379†	335	267	309	316	406	703	465
	1	308	305	541†	332*	241	298	180	280	304	384†	381	331†
Totals		3	4	3	2	7	6	11	5	8	5	3	2

*Record incomplete.
†Only one egg laid; calculation made from time second egg should have been laid.
‡One squab hatched, but died soon.
§Adopted squabs from another nest.
‖Possibly a day or so less.

that it is very infrequently that the birds cease incubating voluntarily by the eighteenth day after the laying of egg B, in case they are allowed to retain unhatched eggs. An inspection of the Table shows, as a matter of fact, that under the conditions specified more birds stop incubating at 23 days than at any other time, and that the number of records falls off from this point in both directions as regularly as could be expected with such small numbers. The

maximum time any birds sat was 28 days,* whereas the mean period which they will sit on the eggs in case they do not hatch, as determined from these 59 records, is 22.69 days. There is therefore a tendency for domestic pigeons, as represented by this group, to incubate the eggs not simply to the mean (17 days), nor indeed to the maximum (20.5 days) time of hatching, but for a somewhat longer period, the average being practically 23 days. The incubating instinct is not, therefore, one exactly adjusted to the number of days required for the young to hatch—such an exact adjustment would in fact be out of the question owing to the considerable variability of this period—but there is rather, as in many instincts and other biological adjustments, a *factor of safety*. Physiological processes in general are characterized by variability, and nature, rather than drawing the line too closely, makes allowance for the extremes. In the present instance the factor of safety may be considered as 6 days, the difference between the mean time of hatching of the second egg and the average time the birds tend to sit. This is fully two days longer than necessary to hatch the eggs which required the longest time (20.5 days) according to our records, and if we may generalize from our data, fully 68% of the birds sit long enough to hatch even the few eggs that reach this limit.

The foregoing data would appear to show conclusively that Raspial was wrong in attributing to the domestic pigeon an exact "notion of the time necessary for incubation" or anything comparable to it. For some years the senior author has desired to test the matter on a wild species, but has had little opportunity to do so. In the spring of 1914, however, with the assistance of Mr. A. R. Cahn, a complete record was made of the laying and incubation of a pair of Mourning Doves (*Zenaidura macroura carolinensis*). The nest was some 12 or 15 feet from the ground on the horizontal branch of a tamarack tree on the campus of the University of Wisconsin. The chronological history of the case is as follows:

*The statement of a maximum of 30 days in a preliminary communication (Cole, 1911) was based on the time of laying of the first egg rather than the second.

May 4, 1914. A pair of Mourning Doves observed "looking over the location;"
            their behavior indicated that they would probably nest soon.
May 7.   Foundation of nest laid at place where birds were previously seen.
May 10.   Nest apparently complete; no eggs; birds not in evidence.
May 12.   First egg laid before 8 A. M. (no record of time of last observation on
            day previous).
May 13.   Second egg laid between 8 and 9 A. M.
May 14.   Birds incubating.
May 23.   Two eggs with dead embryos of Ring dove (*Turtur risorius*) substituted
            for the Mourning Dove eggs; the latter placed in an incubator.
May 26.   Mourning Dove eggs both hatched in incubator during night; period of
            incubation 13 days from laying of second egg.
May 28.   Mourning Doves still incubating.
May 29, 1:30 P. M. Mourning Dove on nest.
May 30, 8:30 A. M. Mourning Dove on nest.
         10:30 A. M. Nest deserted; birds not seen around it thereafter. Still
            contained the substituted eggs, thus showing it was not
            an accident to the eggs which caused the termination of
            incubation.

While this is but a single case, the evidence it furnishes is positive, and there is no reason to believe it is not about what might normally be expected under similar circumstances. The points of interest to us may be summed up briefly:

1.   The period of incubation for both the Mourning Dove eggs was 13 days from the time of laying of the second egg.

2.   The parent birds continued to sit on the substitute eggs for four days after their own eggs had hatched, which is 31 per cent. of the period of incubation of their own eggs. In the domestic pigeons the "factor of safety" was determined as 6 days, or 35 per cent. of the mean period of incubation.

It is interesting to note that desertion of the eggs by the Mourning Doves occurred after 8:30 in the morning and before 10:30. If their habits with respect to the division of labor in incubation are similar to those of pigeons, the male sitting approximately from 10 A. M. to 2 or 3 P. M., this probably means that it was the male bird which first failed to continue the extended incubation of the refractory eggs.

Summary.

Below are summarized the principal conclusions of the present report. Although some of them may here be stated in a rather general form, it is to be kept in mind that they are based wholly on the data which have been presented, and no claim is made for their generality beyond this. Nevertheless it is our *opinion* that they are built on a broad enough foundation to render very probable their general application to domestic pigeons.

Sex ratio.

1. The normal ratio of the sexes of pigeons hatched is 105 males to 100 females (p. 465).

Death rate.

2. The death rate of squabs is especially high for the first two or three days after hatching, and at about 10 to 15 days of age (p. 470).

Differential mortality.

3. When the two squabs are of distinctly different size before the banding age (10 to 15 days) the larger squab is more often a male than a female (p. 467).

4. The death rate for the two sexes, in bisexual broods, is essentially equal (p. 471).

5. There is no marked tendency for one sex to be weaker than the other in bisexual broods, and there is only a slight indication that more males than females from such broods survive to adult life— placed at 6 months (p. 472).

6. A consideration of the ratio of males to females in each of the age groups defined does not indicate a high relative mortality of females in the ages preceding the adult state (p. 473).

7. There is a high mortality of both sexes during the first two or three years of their adult life, and this is especially high in the females between the ages of one and two years (p. 476).

8.   The higher mortality of females at early adult ages, together with the higher proportion of males hatched (105 : 100), may be in large part responsible for the prevailing notion of a considerable excess of male pigeons in adult populations and seems to furnish real substantiation for this notion.   The fact that males are generally more easily recognized than females probably adds to this impression (p. 477).

Ratio of bisexual to unisexual broods.

9.   The number of unisexual broods, in which the squabs are either both male or both female, somewhat exceeds in our records the bisexual broods (one squab of each sex), but the odds against the numbers obtained representing a potential equality are very slight.   These facts are directly contradictory to the statements that the two eggs usually produce a male and a female squab (p. 487).

10.   Considering only the unisexual broods, the number of "both males" to "both females" is practically equal (p. 487).

Sex with respect to order of laying.

11.   A comparison of the numbers of each sex hatched from first eggs and from second eggs respectively, shows no tendency for the former to produce exclusively males and the later females, but as a matter of fact more males than females are hatched from both (p. 487).

Time of laying.

12.   The mean time of laying of the first egg is about 5 P. M., and of the second egg about one o'clock of the afternoon of the second day following (p. 489).

13.   The mean interval between the laying of the two eggs is practically 44 hours (p. 490).

14.   The mean time between the laying of the first and second eggs decreases progressively in the months from February to July, inclusive (p. 491).

15.   There is a very sensible positive correlation between the time of laying of the first and of the second egg.   The equation of the regression curve is given, which enables one to calculate the most probable time of laying of the second egg when the time the first was laid is known (p. 493).

Time of hatching.

16.   The mean time of hatching of the first egg is 16.5 days after the laying of the second (p. 496).

17.   The mean time of hatching of the second egg is 17 days after it is laid (p. 496).

18.   On the average, therefore, the time from laying to hatching of the first egg is nearly a day and a half longer than it is for the second egg.   This is probably to be accounted for by the fact that the first egg receives very little incubation until the second is laid (p. 499).

19.   There is a high correlation between the times of hatching of the two eggs of a clutch (p. 497).

"Control of sex."

20.   So far as the data presented go, they appear to indicate that sex in pigeons is determined according to the laws of chance (p. 501).

Time of sitting.

21.   In case the eggs do not hatch they are seldom abandoned at the end of the normal period of incubation, but the birds continue to sit on them for a time longer (p. 504).

22.   The length of time they will continue to incubate the eggs varies, but averages practically six days after the normal period, making the mean total time of incubation when the eggs do not hatch 23 days after the laying of the second egg (p. 504).

23.   This continuance of incubation beyond the normal time under such circumstances constitutes a "factor of safety" in the incubating instinct (p. 505).

24. A pair of Mourning Doves continued to sit on substituted eggs for four days after their own had hatched in an incubator, thus disproving Raspial's assertion that wild birds have an "exact notion of the time required for the eggs to hatch" (p. 506).

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